THE VEGETATION OF THE FRESHWATER SWAMPS OF INHACA ISLAND

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ABSTRACT

A comparative account is given of the inland freshwater swamps of Inhaca Island, Moçambique. The vegetation is described in general terms and information is given as to the reaction and chloride content of the water and soils of the swamps.

The effects of human activity are described, for it is chiefly due to these influences that the swamps owe their most characteristic features and can no longer be considered to be in a natural condition.

The zonation of the swamps and their surrounds is remarkably uniform. A central zone of open water occupied by *Typha australis* Schum. et Thonn. or *Phragmites communis* Trin. is surrounded by a mixed community of amphibious herbaceous plants. This is in turn enclosed by grassland, which gives way at the outer edges of the swamp to forest. A striking feature is the small number of species present and the almost total absence of truly aquatic plants.

The swamps have no surface drainage. In all cases the chloride content is very low. The water is only slightly acid or even alkaline, but there is a very sharp increase in acidity in the surrounding soil.

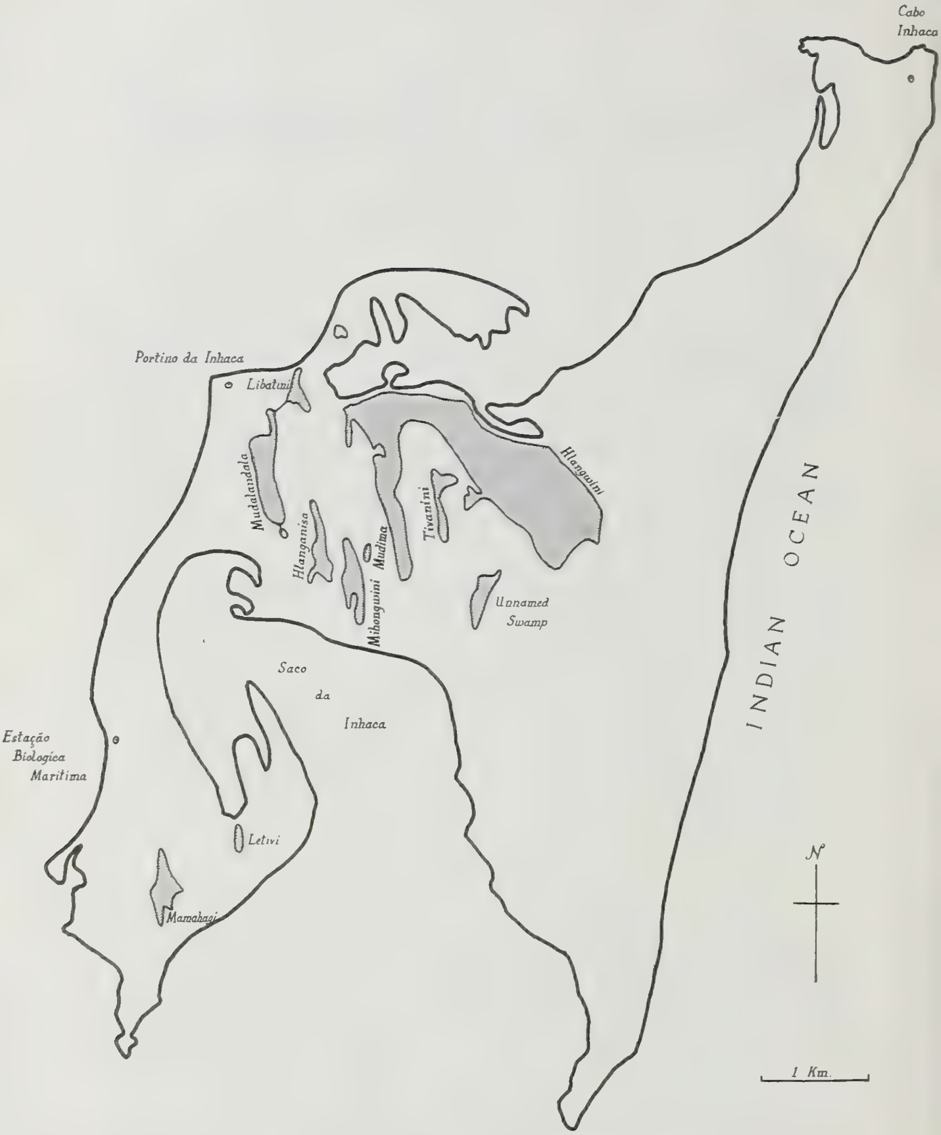
The conclusion is reached that these swamps may be justifiably classified as fens.

INTRODUCTION

Comparatively few accounts exist of the phanerogamic vegetation of freshwater communities of Southern Africa, particularly with respect to tropical or sub-tropical regions. This description of the swamps of Inhaca Island is therefore presented as a contribution towards a more detailed and systematic knowledge of the plant communities of the sub-continent.

Inhaca lies on the 26th parallel, some thirty-five kilometres east of Lourenço Marques. It is therefore in the sub-tropical zone.

The interior of the island is dissected by a complex series of sandy hill ridges, running chiefly in a north-south direction. Many of the valleys between these ridges are occupied by swamps, though the area of open



After H.B.S. Cooke.

FIG. 1.—Map of Inhaca Island, Showing the Position of Freshwater Swamps (Stippled)

water is very restricted. The altitude of the swamps is just above or below ten metres above sea-level. Most of the swamps have Ronga names but some are apparently unnamed.

The swamps are very similar in appearance and general features, but show interesting minor differences of ecology. Nearly all are completely landlocked but, in view of the sandy substratum, the possibility of subterranean drainage cannot be overlooked. The fact that the swamps are established on sand, which indeed covers most of the island, is also a feature of particular interest.

There is little doubt that the swamps are drying up. Mogg (in Moss and Macnae, 1958), describes this process as it has taken place since 1922.

The freshwater swamps are all very strongly influenced by human activity, and the interaction of the vegetation with the biotic factor was most striking in all the swamps examined. The greatest effects are due to the intensive cultivation of the borders of the swamps. The swamp water is utilized for irrigation and to this end channels are cut back into the land surrounding the swamps. Cultivation is carried out right to the edge of the open water of the swamps, so that there has been extensive clearance of the natural marginal vegetation. Old, dried-up swamps are almost entirely under cultivation. Nevertheless, in the wetter places, semi-aquatic vegetation readily re-colonizes unattended or abandoned land, and it is only by constant attention that the ground can be kept clear.

A further important factor is the use of *Imperata cylindrica* (L.) Beauv. for thatching. Many of the swamps are regularly fired to promote the growth of this grass. Having a deeply buried rhizome, it is not killed by the process and regenerates readily.

There are very few livestock on the island and these do not bring about any marked modification of the swamp vegetation. The extensive marginal trampling which is a common feature of swamps and vleis in Southern Africa is here altogether absent. Moreover the gathering of water by the native population of the island results only in the trampling of quite localized areas. In many cases special water holes are dug at the sides of the main swamps so that the latter are unaffected by water gathering.

DESCRIPTION OF THE SWAMPS

1. The Mamahagi Swamp.

This swamp is situated in a wide shallow basin amongst low sand hills. The zonation of the swamp is very conspicuous, comprising the following regions with their associated plant communities:

(*a*) Phragmitetum—Typhetum, in deep water.
(*b*) Shallow open water with few plants.
(*c*) Fringing zone of low-growing reed-swamp plants.
(*d*) Zone of grass associations or cultivation.
(*e*) Forest margin.

The plant communities are remarkably pure and have sharp boundaries.

The centre of the swamp is dominated by *Phragmites communis* Trin., standing in fairly deep water. In parts *Typha australis* Schum. et Thonn. is a co-dominant, but particularly at the northern end and around the outer fringes of the *Phragmites* it occurs as pure stands. The *Typha* and *Phragmites* deposit a litter of dead leaves which are slow to decay and form a thick and stable mat in the shallow water around the edges of the community. This mat encroaches on a region of open water of variable width. The following species were found in this zone and as occasional associates of the Phragmitetum-Typhetum: *Albizzia versicolor* Welw., *Euthalia conyzoides* L. (drier parts), *Hibiscus surratensis* L., *Rhus cf. pyroides* Burch., *Pentodon pentander* (Schum.) Vatke, *Pycreus mundtii* Nees, *Ricinus communis* L., *Blumea caffra* (DC.) O. Hoffm., *Hydrocotyle bonariensis* Lam., *Phyla nodiflora* (L.) Greene, *Nidorella auriculata* DC., *Polygonum acuminatum* H.B.K. var. *capense* Meisn.

The marginal zone of open water is continuous with several ditches which radiate outwards from the swamp. These ditches are water-filled at their inner ends but become progressively shallower and eventually completely dry as they leave the vicinity of the swamp. The following is a list* of the species which occur in the ditches, in order of decreasing wetness:

(*a*) Water up to 46 cm. deep: *Blumea caffra* (DC.) O. Hoffm. (*a*), *Erigeron canadensis* L. (*a*), *Phyla nodiflora* (L.) Greene (*o*), *Veronica anagallis-aquatica* L. (*o*).
(*b*) Water up to 15 cm. deep: *Phyla nodiflora* (L.) Greene (*a*), *Nidorella auriculata* DC. (*f*), *Polygonum acuminatum* H.B.K. var. *capense* Meisn. (*f*).
(*c*) Saturated soil: *Imperata cylindrica* (L.) Beauv. (*a*), *Pentodon pentander* (Schum.) Vatke (*a*), *Fimbristylis ferruginea* Vah.. (*f*), *Euthalia conyzoides* L. (*r*).
(*d*) Soil dry but liable to flooding: *Cryptolepis obtusa* N.E.B. (*a–d*), *Centella coriacea* Nannfd. (*a*), *Pycreus mundtii* Nees (*a*), *Erigeron canadensis* L. (*f*,) *Dactyloctenium gemminatum* Hack. (*f*).

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* Throughout this account the following symbols are used to denote frequency: *d*=dominant, *a*=abundant, *f*=frequent, *o*=occasional, *r*=rare, *v.r.*=very rare.

The outermost zone of the swamp is dominated by grasses and small herbaceous plants. This is well developed only on the western side, elsewhere being extensively cultivated. The following grasses occur in this zone: *Dactyloctenium aegyptum* (L.) Beauv., *Digitaria milanjiana* (Rendle) Stapf., *Eragrostis ciliaris* (L.) R. Br., *Ischaemum arcuatum* (Nees) Stapf. and *Panicum lavaefolium* Hack. *Panicum* is particularly abundant within the shade of the forest margin whilst in wet places *Ischaemum* occurs almost to the exclusion of other species. Other associates of the grass zone are *Asystasia gangetica* (L.) Anders., *Agathisanthemum bojeri* Klotzsch., *Centella coriacea* Nannfd., *Commelina nudiflora* L., *Cryptolepis obtusa* N.E.Br., *Cyperus sphaerospermus* Schrad., *Lobelia senegalensis* L., *Dicerocaryum zanguebarium* (Lour.) Merrill, *Smilax kraussiana* Meisn. *Sonchus oleraceus* L. and *Coccinia rehmannia* Corme. (forma).

The effects of cultivation are clearly shown in the grassland and cleared forest at one side of the swamp, some recently brought into use but elsewhere lying disused and rapidly becoming recolonized by a flora of ephemerals, followed by a strong invasion of swamp and forest species. Radiating out from the swamp are a number of irrigation ditches, some being natural drainage channels which have been deepened whilst others are entirely artificial. The presence of these carries outliers of the swamp vegetation across the dry sandy cultivated areas, and serves to furnish a ready supply of stolons and rhizomes for marginal infestation of these areas. The following species were collected from the cultivated land at the side of the Mamahagi Swamp: *Digitaria milanjiana* (Rendle) Stapf (*a*), *Digitaria swazilandensis* Steut. (*a*), *Eragrostis ciliaris* (L.) R. Br. (*a*), *Fimbristylis exilis* (R. Br.) R. et S. (*a*), *Perotis patens* Gaud. (*a*), *Rhynchelytrum repens* (Willd.) Hubb. (*a*), *Brachiaria humidicola* (Rendle) Schweik. (*a*), *Dipcade viride* (L.) Moench. (*f*), *Erigeron canadensis* L. (*f*), *Phyllanthus delagoensis* Hutch. (*f*), *Centella coriacea* Nannfd. (*o*), *Cyperus tenax* Boek. (*f*), *Sesamum alatum* Thonn. (*o*), *Cassia mimosoides* L. (*o*), *Dicerocaryum zanguebarium* (Lour.) Merrill (*o*), *Cyperus sphaerospermus* Schrad. (*r*), *Helichrysum kraussii* Sch. Bip. (*r*), *Lobelia senegalensis* A. DC. (*r*), *Oxygonum delagoense* O. Kuntze (*r*), *Triumfetta rhomboidea* Jacq. (*r*), *Vernonia poskiana* Vatke (*r*), *Brachiaria deflexa* (Schum.) C. E. Hubb. ex Robyns (*v.r.*), *Crotalaria lanceolata* E. Mey. (*v.r.*), *Hermannia modesta* (Ehrenb.) Manch. (*v.r.*), *Hyparrhenia dissoluta* (Nees) Hubb. (*v.r.*), *Merremia tridentata* (L.) Hall. f. (*v.r.*), and *Nidorella auriculata* DC. (*v.r.*).

On the north-west facing side of the swamp, on dry sandy soil, there is an invasion by *Helichrysum kraussii* Sch. Bip. The site is one of abandoned cultivation and the soil is loose and devoid of humus. *Helichrysum kraussii* Sch. Bip. forms small shrubs 30 to 60 cm. in height scattered at 60 to 90 cm. intervals. Thus whilst the plants are young the soil is quite exposed. Later a closed canopy of *Helichrysum* is formed in many places, but even then the soil is quite unstable until an undergrowth of other shrubs and also small trees becomes established. Elsewhere on the island the remaining stages of the succession may be seen, where there is regeneration to natural scrub forest. The herbaceous associates of *Helichrysum kraussii* at the Mamahagi Swamp are: *Cyperus tenax* Boeck. (*a*), *Fimbristylis exilis* (R. Br.) R. et S. (*a*), *Indigofera preladoi* Harms. (*f*), *Dactyloctenium aegyptum* (L.) Beauv. (*r*), *Dicerocaryum zanguebarium* (Lour.) Merrill (*r*), *Rhynchelytrum repens* (Willd.) Hubb. (*v.r.*) and *Urochloa stolonifera* (Goosens) L. Chipp. (*v.r.*).

The swamp is surrounded by forest which forms a sharp boundary to the grassland and cultivated areas. The commonest species of the forest margin are: *Albizzia gummifera* (Gmel.) C. A. Sm., *A. versicolor* Welw., *Chrysanthemoides monolifera* (L.) T. Norl., *Oncoba kraussiana* Planch., *Conopharyngia elegans* (Stapf.) Stapf., *Strychnos spinosa* Lam., *Phoenix reclinata* Jacq., *Trichilia roka* (Forsk.) Choiv. and *Syzygium cordatum* Hochst., with *Cissampelos pareira* L. climbing over the outermost shrubs.

The soil of the swamp margin, though sandy, is rich in humus and of a dark colour whilst the surrounding regions have a soil which is highly leached and almost white. There is a sharp increase in acidity in passing from the wet to the dry soil, as is shown in Table I.

The water of the swamp is faintly brak but, as would be expected from its very light and sandy nature, no chloride could be detected in the surrounding soil.

TABLE I

REACTION AND CHLORIDE CONTENT OF SOIL IN THE MAMAHAGI SWAMP.

Origin of Sample	pH	Chloride
Centre of swamp (water sample)	8·0	42 p.p.m.
Edge of Typhetum; soil black and sticky, lying under 0·3 m. of water	8·0	29 p.p.m.
5·5 m. from edge of water: soil black in colour and sandy; cultivated	6·6	absent
11·0 m. from edge of water; soil light brown in colour, sandy and moist; cultivated	5·9	absent
16·5 m. from edge of water; old cultivated soil	5·9	absent
Ischaemetum: old cultivated land	5·8	absent
23·8 m. from edge of water; soil very light brown in colour, of loose sand. Forest margin	5·6	absent

All chloride determinations were carried out by Best's electrometric method. Soil and water reaction was determined in the field by the method of Kuhn.

2. WESTERN ARM OF HLANGWINI SWAMP.

The centre of the swamp is occupied by a pure stand of *Typha australis* Schum. et Thonn. This is surrounded by a zone in which *Typha* is still dominant but has amongst it scattered plants of *Phragmites communis* Trin. This is in turn enclosed by co-dominant *Typha* and *Phragmites* with a conspicuous under-storey of *Polygonum acuminatum* H.B.K. var. *capense* Meisn. and *Melanthera scandens* (Schum. et Thonn.) Brenan., the latter reaching a height of about four feet above the water surface. The swamp is surrounded by a marginal ditch, a very constant feature of the Inhaca swamps, in which flourishes a luxuriant herbaceous vegetation. In this case there is some thinly scattered *Phragmites* and a thick carpet of *Dryopteris gongylodes* (Schk.) Ktze. In some parts of the swamp the latter occurs pure, in other parts *Commelina, Jacquemontia tamnifolia* (L.) Griseb. and *Pentodon pentander* (Schum.) Vatke are associated with it. On the drier side of the ditch, that is, away from the main body of the swamp, *Panicum maximum* Jacq., *Hydrocotyle bonariensis* Lam., *Imperata cylindrica* (L.) Beauv. and *Helichrysum foetidum* (L.) Cass. occur.

The west side of the swamp is bordered by cultivated land, but the east side shows typical marginal grassland·up to the edge of the forest. This grassland includes *Ischaemum arcuatum* (Nees) Stapf., *Cassia mimosoides* L., *Cyperus sphaerospermus* Schrad. and *Imperata cylindrica* (L.) Beauv.

3. THE MUDALANDALA SWAMP.

This is a large swamp dominated by *Typha australis* Schum. et Thonn. with no *Phragmites* present. Of particular interest is the occurrence of *Cyperus papyrus* L. which is found nowhere else on the island. The *Typha* grows right up to the edge of the marginal ditch and extends in a rather scattered fashion up to the lateral ditches.

The land surrounding the swamp is cultivated, but there remains the characteristic narrow wet zone fringing the swamp itself. Aquatic vegetation extends for about twenty to forty feet up the radiating side ditches. This includes *Commelina nudiflora* L., *Dryopteris gongylodes* (Schk.) Ktze., *Torenia thouarsii* (Cham. et Schlecht.) Kuntze, while in the drier parts further from the swamp *Hydrocotyle bonariensis* Lam., *Lobelia senegalensis* A. DC., *Pentodon pentander* (Schum.) Vatke and *Polygala rehmanni* Chodat. are found.

The main swamp drains northwards towards the sea by way of a narrow marshy stream. The centre of this stream is occupied by *Typha australis* Schum. et Thonn. On either side is an inner zone of *Dryopteris gongylodes* (Schk.) Ktze. and an outer zone of *Cyperus aequalis* Vahl., both with associated *Polygonum acuminatum* H.B.K. var. *capense* Meisn.

The narrow swamp just described widens out into the Libatini Swamp which lies near to the coast. It is occupied almost entirely by *Phragmites communis* Trin.

The south end of the Mudalandala Swamp shows the following structure: The central part is occupied by *Typha australis* Schum. et Thonn. with an understorey of *Dryopteris gongylodes* (Schk.) Ktze. and *Polygonum acuminatum* H.B.K. var. *capense* Meisn. There is a marginal zone in which *Dryopteris* is dominant. Associated species are *Polygonum acuminatum* H.B.K. var. *capense* Meisn., *Cyperus aequalis* Vahl., *Jussiaea pilosa* H.B.K. and a little *Typha australis* Schum. et Thonn. A wide ditch forms the edge of the swamp in this region. The inner, wetter side is dominated by *Cyperus aequalis* Vahl. with occasional *Xyris anceps* Lam. and *Commelina diffusa Burm f.* whilst the outer side of the ditch, which borders on sandy cultivated land, bears *Imperata cylindrica* (L.) Beauv. as a dominant, and *Gomphocarpus fruticosus* (L.) Ait., *Eriosema parviflorum* E. Mey. and *Torenia thouarsii* (Cham. et Schlecht.) Ktze., which is confined to the upper edge of the ditch.

The water of the swamp has a pH of 4·6 and a chloride content of 4 p.p.m.

4. Unnamed Swamp.

This is a large swamp lying in a wide shallow valley between the hills to the north-east of the Saco. The southern end is extensively cultivated, with little square patches of mannihot cut out from the swamp and irrigated by a complicated system of ditches. Twelve hours after rain these ditches remained full of water and the surrounding soil was saturated in spite of its loose sandy nature. These patches of cultivation are of different ages, the most recently developed having a thin cover of ephemeral weeds whilst the older have been recolonized by swamp vegetation, notably *Ischaemum arcuatum* (Nees) Stapf. and *Pentodon pentander* (Schum.) Vatke.

The swamp is completely surrounded by rising ground which bears forest or forest remnants and broad tracts of grassland.

A small area at the south end of this swamp is still in a fairly natural condition, with open water. This is probably the remnant of a much larger swamp. The dominant species are *Typha australis* Schum. et Thonn., *Dryopteris gongylodes* (Schk.) Ktze. and *Polygonum acuminatum* H.B.K. var. *capense* Meisn. Around the edge of this small area are found *Ischaemum arcuatum* (Nees) Stapf., *Imperata cylindrica* (L.) Beauv., *Cyperus isocladus* Kunth., *Gomphocarpus fruticosus* (L.) Ait., *Fuirena* *chlorocarpa* Ridl. and *Nymphaea capensis* Thb. There is the usual water-filled ditch which leads off into channels between raised islands of cultivation or *Ischaemum.*

The greater part of the main swamp, that is the large area north of the Typhaetum and cultivated plots, is covered by a dense sward of *Ischaemum*, with occasional plants of *Cyperus obtusiflorus* Vahl. and *Periglossum mossambicense* Schltr.

The water of the *Typha* swamp has a reaction of pH 7 and a chloride content of 7 p.p.m. The Ischaemetum is developed in waterlogged, black sandy soil with a pH of 6·4 and a chloride content of 3 p.p.m. The much drier soil at the outermost edge of the Ischaemetum has a pH of 5·7 but contains no detectable chloride.

5. The Mihongwini Swamp.

This swamp is situated in a rather steeper-sided bowl than the others but still has the usual marginal forest followed by grassland or cultivated plots surrounding the swamp proper.

The central part of the swamp is occupied by pure *Typha australis* Schum. et Thonn. growing in fairly deep water. A very well-marked zone of herbaceous dicotyledons grows in the shallow water at the edge of the swamp. It contains scattered plants of *Typha* and in addition the following species are present: *Triumfetta pilosa* Roth., *Dryopteris gongylodes* (Schk.) Ktze., *Polygonum acuminatum* H.B.K. var. *capense* Meisn., *Melanthera scandens* (Schum. et Thonn.) Brenan, *Fuirena chlorocarpa* Ridl., *Psoralea, Torenia thouarsii* (Cham. et Schltr.) Ktze., *Pentodon pentander* (Schum.) Vatke, *Euthalia conyzoides* L. and *Ischaemum arcuatum* (Nees) Stapf., the latter rather sparse and very tall when growing in water.

There is a second zone of herbaceous plants outside the inner one, and this is readily recognizable not only because of a distinct species list but also by the much drier substratum. It is occupied by *Ischaemum arcuatum* (Nees) Stapf., *Hydrocotyle bonariensis* Lam., *Imperata cylindrica* (L.) Beauv., *Torenia thouarsii* (Cham. et Schltr.) Ktze. and *Cassia mimosoides* L. *Limeum viscosum* s.sp. *viscosum* var. *kraussii* occurs in the damp borders of the cultivated land. There follows then what may be described as the dry Ischaemetum with *Eriosema parviflorum* E. Mey. and *Fuirena.*

At one side of the swamp the marginal ditch is absent, and here one can see what may well be the more natural border of these swamps. A zone occurs dominated by *Dryopteris gongylodes* (Schk.) Ktze. with which are associated scattered *Typha, Polygonum acuminatum* H.B.K. var. *capense* Meisn. and *Melanthera scandens* (Schum. et Thonn.) Brenan.

These plants form a raised mat, where the soil is waterlogged but not submerged.

As in most parts of the island, the soil of the surrounding cultivated land is of very loose leached sand, with *Gisekia pharnaceoides* L. occurring frequently. The soil reaction and chloride content bear a similar relationship to the proximity of the wet part of the swamp that they do elsewhere. Thus the swamp water has a pH of 6·6 and chloride content of 13 p.p.m. Soil from the emersed *Dryopteris* zone has a pH of 5·7 and chloride content of 3 p.p.m., whilst similar measurements for the dry Ischaemetum are pH 5 and chloride content 1 p.p.m.

The Mihongwini Swamp has no free-floating or floating-leaved specimens, possibly due to the shading and overcrowding by the tall reed swamp plants. The swamp shows marked vertical stratification. Thus the dominant *Typha australis* Schum. et Thonn. rises to a height of about 2·7 m. above the submerged mud surface. *Dryopteris* and *Polygonum* form a fairly open canopy beneath the *Typha*. The depth of water varies, but in general the submerged parts of the reedswamp plants are enclosed by dead leaves in different stages of decomposition. These not only float on or just below the surface, but remain entangled with the growing stems to form a continuous loose mat to the bottom.

As has been indicated, there is no marginal ditch in some parts of the Mihongwini Swamp, and under these circumstances a mat of vegetation forms above the water. Even on moderately moist soil there is similar stratification and there is formed a dense cushion, 90—120 cm. thick, of living and non-living stems and leaves of *Dryopteris*, *Polygonum* and *Cyperus sphaerospermus* Schrad. The latter is dominant and contributes towards knitting together the cushion of vegetation by virtue of its stoloniferous and viviparous mode of growth. The ground beneath is covered by a thick layer of brown, semi-humified débris. It has a reaction of pH 6·8 and a chloride content of 7 p.p.m., so that in this respect it constitutes a substratum with greater affinities with the centre of the swamp rather than with the surrounding land. Though the surface is dry and firm enough to walk on, the water may be only one inch below. The soil underlying this litter is sandy, blackish brown in colour and sweet smelling, as contrasted with the malodorous black muddy sand found in the centre of all the swamps.

6. HLANGANISA SWAMP.

Phragmites communis Trin. is the dominant plant of the deep water occupying the centre of the swamp, but there are pools and channels of open water in which grow one of the few floating-leaved aquatics which occur on the island, *Nymphaea capensis* Thb. The Phragmitetum is surrounded by a marginal zone of vegetation on wet soil or in shallow water. This zone may be subdivided into distinct inner and outer regions. The former is dominated by *Phragmites*, with *Cladium jamaicense* Crantz. and *Dryopteris gongylodes* (Schk.) Ktze. as associates. In the outer zone *Dryopteris* becomes dominant and is accompanied by *Polygonum acuminatum* H.B.K. var. *capense* Meisn., *Melanthera scandens* (Schum. et Thonn.) Brenan. and a little scattered *Phragmites*. (Fig. 2.)

The swamp is bounded by a wide shallow ditch. The inner, swamp, side is occupied by the previously mentioned species of the marginal zone whilst the outer side, which comes under the influence of cultivation, carries a number of water-loving weeds very similar to those described from the Mamahagi Swamp. Ditches which traverse the cultivated areas also carry a water-tolerant flora, such as *Imperata cylindrica* (L.) Beauv., *Pentodon pentander* (Schum.) Vatke, *Erigeron canadense* L. and also *Helichrysum foetidum* (L.) Cass. for a limited distance.

The reaction and chloride content of the swamp water and soil is shown in Table II. Once again it will be noticed that there is an increase in acidity and a decrease in chloride in passing from the wetter parts of the swamp to the surrounding drier soil.

TABLE II

REACTION AND CHLORIDE CONTENT OF SOIL IN THE HLANGANISA SWAMP

Origin of Sample	pH	Chloride
Swamp water	8·0	22 p.p.m.
Inner marginal zone, soil	7·5	9 p.p.m.
Outer marginal zone, soil	7·5	4 p.p.m.
Ditch, submerged soil	7·0	2 p.p.m.
Ditch, top edge bordering cultivation	5·8	absent
Cultivated soil 3·7 m. from water	5·5	absent

7. SOUTH END OF THE MUDALANDALA SWAMP.

At the south end of the Mudalandala is a small swamp which appears to drain into the main swamp, partially by way of a short stream but otherwise underground. The distance between the large and small swamp is about 275 m.

The water of the small swamp is very foul and the dominant vegetation consists of *Phragmites*. The zonation, extending from the stream at the north end, is as follows: There is a patch of pure *Dryopteris gongy-*

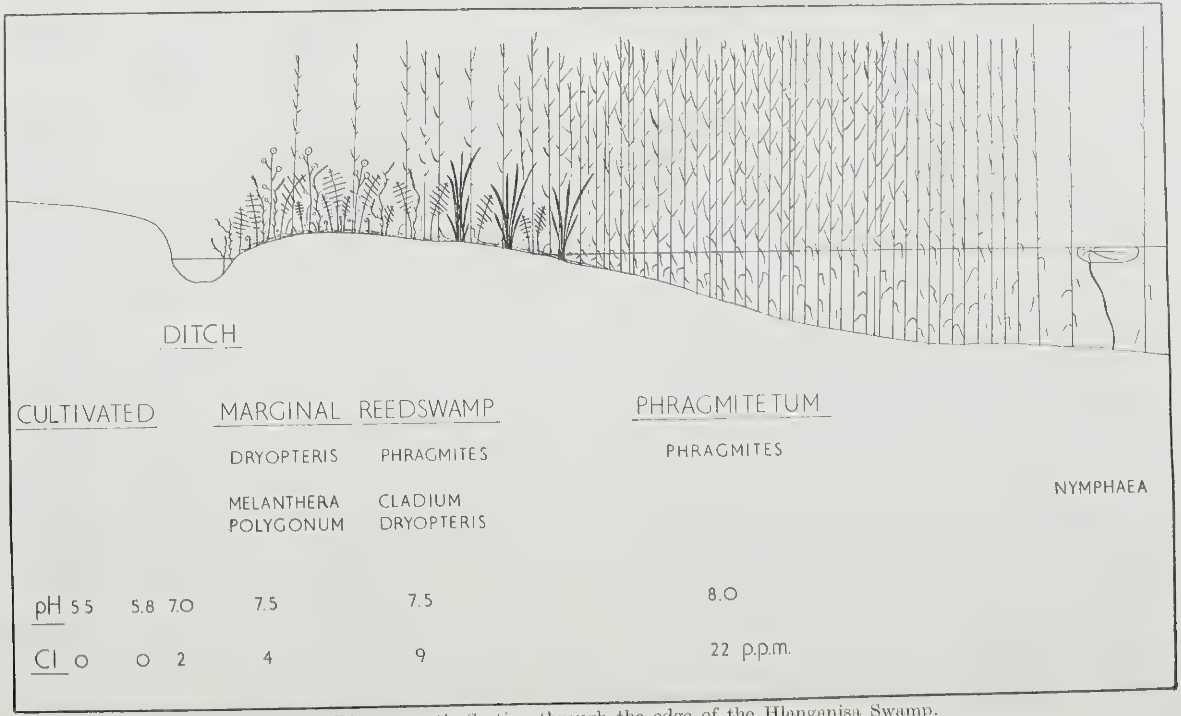

Fig. 2.—Diagrammatic Section through the edge of the Hlanganisa Swamp.

lodes (Schk.) Ktze. followed by some *Phragmites* with scattered *Typha* and *Melanthera*. The central channel of open water contains a thin cover of *Phragmites*, with *Melanthera scandens* (Schum. et Thonn.) Brenan, *Polygonum acuminatum* H.B.K. var. *capense* Meisn. and *Imperata cylindrica* (L.) Beauv. On either side of this *Phragmites* is dominant though very thinly distributed. The wet marginal zone is present as in other swamps described, but it is not sharply demarcated. The water of this swamp has a pH of 7·4 and a chloride content of 28 p.p.m. A feature of particular interest is the presence of *Pteridium aquilinum* (L.) Kuhn. at the southern end. This plant at present extends to within 60 cm. of the outermost scattered *Phragmites*, though it is on sloping ground and does not reach very wet soil.

THE GENERAL FEATURES OF THE SWAMPS

The freshwater swamps of Inhaca Island are very uniform in structure. In all cases there is a central region of shallow water occupied by a reed-swamp community. There is an almost total absence of submerged aquatic plants, *Utricularia stellaris* L. f. being one of the few exceptions. *Nymphaea capensis* Thb. and *Lemna minor* L. are the only floating-leaved aquatics recorded, and even these have very sporadic distribution. As compared with the freshwater communities described from the Union of South Africa, the number of species recorded from the swamps of Inhaca is rather restricted, being about fifty species. The sparsity of species is undoubtedly due to shading of the water by the dominant or co-dominant plants. Though the water is not turbid and never more than faintly brown-tinged, the bottom is rich in humus and the water therefore almost certainly presents an oxygen-deficient habitat.

All the swamps are sited on sand but, except where cultivated, a considerable depth of sandy peat is developed. In most cases there is no free drainage. A characteristic feature is the presence of a peripheral water-filled ditch, artificially kept open. The Phragmitetum and particularly the Typhetum in the central region of the swamps is characterized by a mat of dead leaves. This forms a floating platform upon which it is possible to walk dryshod. This obviously is highly effective in preventing any illumination of the water beneath and deters any but the most vigorous competitor from becoming established.

In spite of apparently rather uniform conditions throughout the island, there is a remarkable dissimilarity between the floras of the different swamps. Thus *Nymphaea capensis* Thb. occurs in one swamp only, *Lemna minor* L. in one small water hole, *Phyla nodiflora* (L.) Greene and *Blumea lacera* DC. have been found only in the Mamahagi Swamp and *Cladium jamaicense* Crantz. is equally local. *Cyperus papyrus* L. only occurs in the Mudalandala Swamp. *Glinus oppositaefolius* (L.) A. DC. has been collected from a single shaded water hole but not from any of the large swamps.

These differences are possibly due to the complete lack of communication between the swamps by means of streams or other forms of open drainage. The numerous and extensive swamps in the northern half of the island, though frequently much less than half a kilometre apart, are isolated from one another by sandy ridges covered by grass or forest or in other cases cultivated.

The accompanying diagram depicts the generalized structure of these swamps. (Fig. 3.)

There is little evidence of the natural sequence of succession, chiefly because of extensive cultivation of the margins of the swamps. Thus silting up is partially prevented and the swamps tend to assume a convex profile. There is little encroachment by the land vegetation and woody plants are very rare in the immediate vicinity of the swamps. Even *Phoenix reclinata* Jacq., which is frequent throughout the island, only occurs where the forest has been cleared from the edges of the swamps. A single plant of *Rhus. cf. pyroides*, some four feet in height, was found in the Mamahagi Swamp and there is in the same situation a large tree of *Ficus capensis* Thb. These are probably remnants of the boundary between the forest and the swamp.

The secondary sere can be seen in many places. With cessation of soil disturbance the ground in the vicinity of the swamps is invaded by *Ischaemum arcuatum* (Nees) Stapf., although this appears to be a plant of intermediate water tolerance, not being dominant where there is free water nor yet occupying very dry ground. A second system of succession involves the encroachment of forest upon the marginal cultivated land. *Helichrysum kraussii* Sch. Bip. is the forerunner of large shrubs and tree seedlings. *Anacardium occidentale* L. is abundant in the cultivated land around the swamps, and *Syzygium cordatum* Hochst. and *Strychnos spinosa* Lam. survive felling and are left undisturbed on drier ground. Most of the other invaders of cultivated land are those which are common throughout the island and only those in the immediate vicinity of ditches or the swamps show aquatic features.

There is some evidence to suggest that the swamps on Inhaca Island may be classified as fens, in the sense of the European ecologists (*vide* Tansley 1949). Very few fens have been described in Southern Africa, one example being the coastal lakes near Knysna (Martin 1956) which are much more typical and easily recognizable than those on Inhaca. An interesting comparison may be made with the swamps of Huleh,

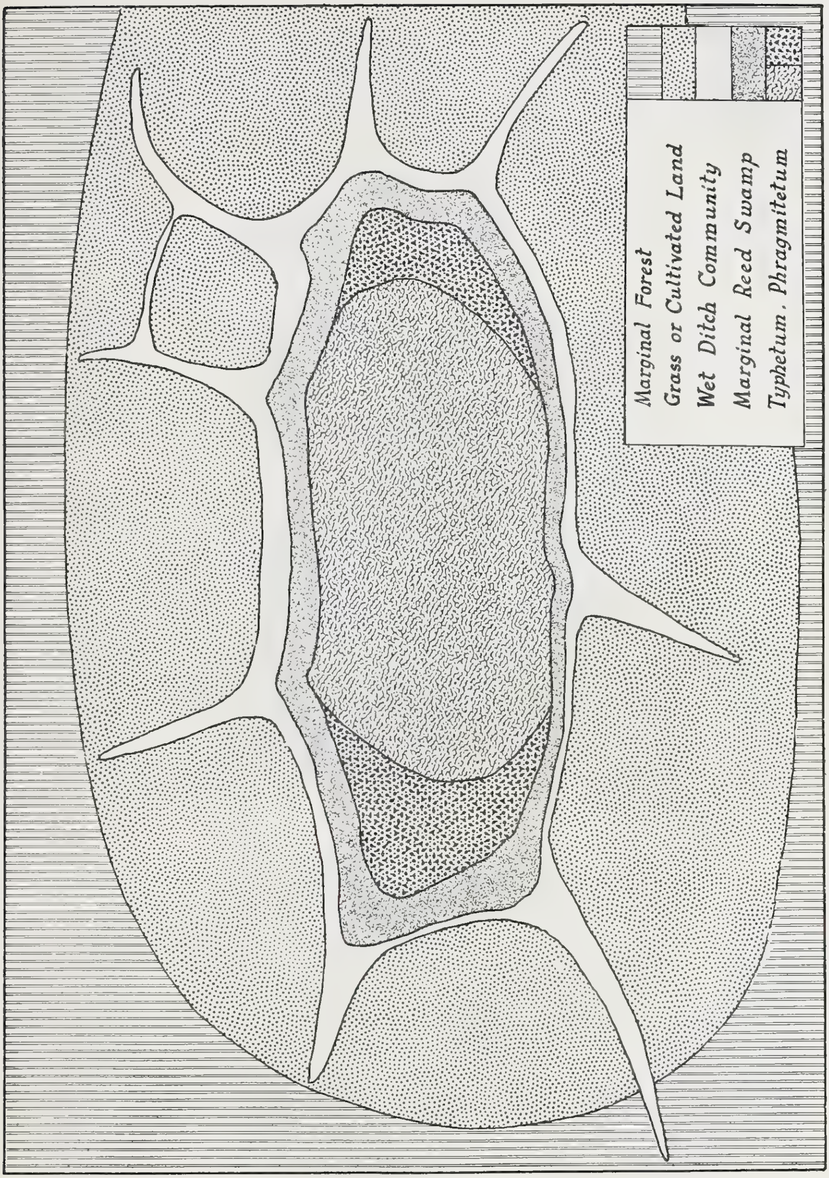

Fig. 3.—Diagrammatic Plan of a Freshwater Swamp on Inhaca Island. (Based on the Mamahagi Swamp.)

Palestine, described by Forbes Jones (1940). There one finds consociations of *Phragmites*, *Typha angustata* Bory et Chaub., *Cyperus papyrus* L. and *Cladium mariscus* R. Br. on alkaline peat. These are regarded as belonging to the fen type of association. The general morphology of these swamps and the species which occur there show many features in common with the Inhaca swamps.

Most of the swamps which have been investigated on Inhaca have water which is neutral or alkaline in reaction, only that of the Mihongwini Swamp being slightly acid and part of the Mudalandala being strongly acid. The soils of the marginal reedswamp also have a reaction that is in most cases not far from neutrality. The chloric contents of the waters are too low to account for any great excess of sodium ions so that one may suppose that the swamps receive calcareous leachate from the surrounding sandy soil. It is noteworthy that the swamps are devoid of halophytes, which might be expected to be associated with saline alkaline soils. Such plants, as for example *Chenopodium vulvaria* L., occur on the fringes of the nearby salt marshes.

Another feature which indicates fen affinity is the formation of neutral peat in the Mihongwini Swamp. The presence of a fringing vegetation of mixed reedswamp species, the marginal ditch of open water and the tendency towards the development of a convex profile to the edges of the swamps are characteristics which conform to general fen type of topography. Very little is known of the autecology of most of the species encountered in these swamps, but *Phragmites communis* Trin. and *Typha* spp. are common dominants of European fens and *Cladium mariscus* R. Br., which is considered to require a soil of at least pH 6 (Conway 1942) is, under north temperate conditions, a fen indicator. *Cladium jamaicense* Crantz. which occurs on Inhaca, is obviously closely allied to the European species and has only recently come to be regarded as distinct.

The swamps on Inhaca do not correspond exactly with any of those previously described from South Africa, though in most cases a comparison is only possible on a basis of the species lists for the different seral stages (Muir 1929, Phillips 1931, Dyer 1937, Louw 1951, West 1951). *Phragmites communis* Trin. appears ubiquitous and *Typha capensis* Rohrb. or *Typha australis* Schum. et Thonn. are constant associates. The interaction of *Phragmites* and *Typha* has been discussed by Phillips (l.c. p. 109) and Louw (l.c. p. 18) and observations at Inhaca confirm the mutual independence of these plants and their very variable behaviour. Either may form pure stands or become associated to any degree, including codominance. *Phragmites* seems to have a rather wider range, extending from deep to very shallow water or even wet soil.

The Inhaca swamps are in an advanced stage of development and, as compared with other swamps described from South Africa, the truly aquatic phase is poorly represented. The zones dominated by members of the Cyperaceae (Muir l.c. p. 70, Louw l.c. p. 21, Phillips l.c. p. 112) are absent. Apart from the few ubiquitous species mentioned above, the species list for the Inhaca swamps have very little in common with those recorded from South Africa, making comparison difficult. Thus *Dryopteris gongylodes* (Schk.) Ktze., which is so prominent on Inhaca, replaces *D. thelypteris* (L.) A. Gray, of South African swamps and *D. thelypteris* (L.) A. Gray, *D. cristata* (L.) A. Gray, etc., of European fens. Members of the Juncaceae are rare.

Thus the Inhaca swamps represent a definite type of community, differing from but yet having affinities with other hydroseres of the temperate regions of the northern and southern hemispheres. This general survey sheds some light on the autecology of certain sub-tropical species, the nature of their associates and their reaction to the biotic factor.

ACKNOWLEDGMENTS

The author wishes to record his wholehearted appreciation of the excellent facilities so generously provided by the Department of Marine Services of Moçambique, and in particular to thank Captain Moeira Rato and Mr. Cravo for their friendly co-operation and assistance throughout his visits to Inhaca Island. To the staff of the Division of Botany, Pretoria, and to Mr. A. O. D. Mogg, the author is indebted for assistance in the identification of specimens. The receipt of a grant towards travel and maintenance expenses from the Council for Scientific and Industrial Research is gratefully acknowledged.

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